PHYLOGENETIC ANALYSIS OF THE SOUTH AFRICAN GENUS *SPARAXIS* (INCLUDING *SYNNOTIA*) (IRIDACEAE–IXIOIDEAE), WITH TWO NEW SPECIES AND A REVIEW OF THE GENUS[1]

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ABSTRACT

Restricted to the western Cape Province of South Africa, *Sparaxis* comprises 13 species of small seasonal geophytes, seven belonging to section *Sparaxis* and six to section *Synnotia*. Until now treated as a separate genus, *Synnotia* is separable from *Sparaxis* section *Sparaxis* (i.e., *Sparaxis* sensu stricto) only by the degree of zygomorphy of their flowers. Species of the two sections have similar karyotypes with $x = 10$; specialized scarious, brown-streaked bracts; an unusual leaf anatomy in which the leaves lack marginal sclerenchyma but have a specialized, heavily thickened marginal epidermis; and similar fruit and seed characteristics. Vegetatively, they have a common gestalt and cannot be distinguished. In section *Sparaxis* the perianth is always actinomorphic, but in two species the stamens are asymmetrically arranged with the anterior stamen opposed to the posterior tepal and the style curved behind it. In section *Synnotia* the stamens are unilateral and arcuate with parallel, contiguous anthers, and the perianth is zygomorphic. Maintenance of *Synnotia*, based solely on this minor distinction, is unacceptable and is inconsistent with the variation in several other genera of Iridaceae–Ixioideae, for example, *Babiana*, *Gladiolus*, *Lapeirousia*, *Watsonia*, *Geissorhiza*, and *Tritoniopsis*, all of which include species with either actinomorphic or medianly zygomorphic flowers. Cladistic analysis of *Sparaxis* using either *Tritonia* or *Ixia* as outgroups for character polarization produces the same internal configuration, but it is more parsimonious to regard *Tritonia* as the immediate outgroup, unless characters such as karyotype are weighted. Cladistic analysis shows that the species clusters recognized as section *Synnotia* and section *Sparaxis* are not phylogenetically equivalent; the two sections are thus recognized for their taxonomic utility.

Restricted to the winter-rainfall region of southern Africa, *Sparaxis* is a genus of small geophytic perennials with cormous rootstocks, a fan of fairly succulent leaves, few-flowered spikes of large, usually brightly colored flowers, and scarious, brown-streaked, long-cuspidate bracts. Until now regarded as comprising just six species with completely regular perianths (Baker, 1896; Goldblatt, 1969), *Sparaxis* is here expanded to include *Synnotia* as section *Synnotia*. As a genus, *Synnotia* is distinguished from *Sparaxis* only by having flowers with a zygomorphic perianth with an enlarged upper tepal. Including *Synnotia*, in which Lewis (1956) recognized five species, and adding two new species, *Sparaxis maculosa* (sect. *Sparaxis*) and *S. caryophyllacea* (sect. *Synnotia*), there are now 13 species of *Sparaxis* and four subspecies.

HISTORY AND RELATIONSHIPS

The close relationship between *Synnotia* Sweet and *Sparaxis* Ker has been generally acknowledged (Baker, 1896: 134; Lewis, 1956) and, when first described in 1804 by John Bellenden Ker (Ker-Gawler), *Sparaxis* included two of the species later to be assigned to *Synnotia* by Robert Sweet (1826). In Lewis's (1956: 138) revision of *Synnotia*, she echoed Baker's comment in *Flora Capensis* that *Synnotia* differed from *Sparaxis* [only] in its irregular perianth. Although all the species

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of *Sparaxis* sensu Goldblatt (1969) have an actinomorphic perianth, the filaments of *S. grandiflora* and *S. bulbifera* are unilateral, the abaxial stamen is curved to lie opposite the adaxial tepal, and the style is displaced to lie between this stamen and the adaxial tepal. In *Synnotia*, the perianth is zygomorphic with at least the upper tepal enlarged and differentiated from the other five, and the stamens are unilateral with the lateral filaments lying close to the displaced abaxial stamen so that the anthers are parallel and more or less contiguous. The difference in zygomorphy between *Synnotia* and the above two *Sparaxis* species is one of degree and is not a valid criterion for generic separation. In other genera of Iridaceae, for example, in *Babiana* and *Gladiolus*, both indisputedly monophyletic genera, there are several species with completely actinomorphic flowers and a greater number with zygomorphic flowers (Lewis, 1959; Lewis et al., 1972). *Watsonia* and *Tritoniopsis* each have a single actinomorphic species that is often segregated subgenerically (Lewis, 1958; Goldblatt, 1989) or sectionally from its zygomorphic congeners. There are similar examples in *Lapeirousia*, *Geissorhiza*, and *Tritonia*. It is clear that zygomorphy has evolved repeatedly in several monophyletic lines in Iridaceae-Ixioideae and may even have been lost in some cases (Hilliard & Burtt, 1991: 36): it is therefore an unsound criterion for the recognition of a genus. This is particularly so in the case of *Sparaxis* and *Synnotia*, where there is a clear progression from actinomorphy to complete floral zygomorphy.

Sparaxis and *Synnotia* are so similar vegetatively that they cannot be distinguished except in flower. The floral bracts, often good indicators of relationship in Ixioideae, are similarly specialized in both. They are scarious and more or less pale-membranous but are irregularly streaked with brown, and are often lacerate and long-cusped. Similar bracts occur in the tropical and southeastern African *Dierama*, for which reason it has been considered related to *Sparaxis*. In *Ixia*, thought to be closely related to *Dierama* (Lewis, 1962), the bracts are usually pale-membranous and short-cusped. These four genera have angular to globose seeds with a surface in which the outline of the epidermal cells is nearly to completely obliterated, a fairly typical seed type in Ixioideae. In *Sparaxis* and *Synnotia* the seeds are completely spherical and perfectly smooth.

Lewis assigned *Synnotia* together with *Sparaxis*, *Streptanthera*, *Ixia*, and *Dierama* to subtribe Ixiinae of the Ixieae. Since then composition of Ixiinae has not changed except that *Streptanthera* and *Sparaxis* are considered congeneric (Goldblatt, 1969). Lewis's treatment was supported by karyology (Goldblatt, 1971: 412), all genera having $x = 10$ and a similar karyotype of small chromosomes.

Studies of leaf anatomy (Rudall & Goldblatt, 1991) have now cast doubt on the validity of Ixiinae. Several genera of Ixioideae have a derived leaf margin structure with columnar epidermal cells with very thick anticlinal walls and without subepidermal sclerenchyma. These include *Sparaxis* (and *Synnotia*), *Crocosmia*, *Chasmanthe*, most species of *Tritonia* (a few have marginal epidermal cells matching those of the laminar epidermis), *Freesia*, and *Anapalina*. *Tritoniopsis* (Goldblatt, 1990; Rudall & Goldblatt, 1991) has columnar and thickened marginal epidermis, but some species also have subepidermal marginal sclerenchyma. *Ixia* and *Dierama* have unmodified marginal epidermal cells and subepidermal sclerenchyma, both considered basal features for Iridaceae. In addition, *Dierama* has an unspecialized leaf anatomy, and its leaves usually lack midribs. In this paper I develop a phylogeny of *Sparaxis* using both *Ixia–Dierama* and *Tritonia* as possible outgroups for polarizing characters. The choice of outgroup makes no difference to the structure of the tree (although the evolution of some characters differs), and the immediate generic relationships of *Sparaxis* remain uncertain.

Review of Taxonomic Characters and Character Polarization

CORM TUNICS

In most species the relatively small corms are enclosed in fine, pale, netted fibers, which outgroup comparison with either *Tritonia* or *Ixia* suggests is the basal condition. In section *Synnotia*, *S. roxburghii* and *S. galeata* have the tunic extending upward in a neck around the base of the plants and the tunics accumulate in an unusually dense mass, particularly in the latter. In *S. villosa*, *S. caryophyllacea*, and *S. variegata* the corm tunics are composed of thicker and harder fibers, especially thickened below, thus resembling claws. This tunic structure is probably an important specialization and is evidence for uniting these three species in a single clade.

LEAVES

Difficult to describe objectively, the leaves of *Sparaxis* can usually be distinguished from other Iridaceae in their somewhat succulent (soft but

firm) nonfibrotic texture. They are always a rather pale green, and the fine, pale lateral veins are perhaps part of the reason for their being easily recognized. In sunlight the leaves seem sprinkled with gold, probably a reflection of the light from the epidermal papillae. Most species of the genus also have obtuse leaves generally obliquely apiculate, unlike both possible outgroups in which the leaves are acute. These leaf characters probably have a basis in internal anatomy, but in any event should be regarded as derived. The leaf margin epidermis of the several species examined anatomically is unusual. As in the case of *Tritonia* and its close allies *Crocosmia* and *Chasmanthe* (de Vos, 1982, 1984) and *Tritoniopsis* (Goldblatt, 1990), the marginal epidermal cells differ from the laminar epidermal cells, being columnar and heavily thickened on the anticlinal walls. The margins lack subepidermal sclerenchyma, as do the margins in the *Tritonia* group but not *Tritoniopsis* (Goldblatt & Manning, 1990; Rudall & Goldblatt, 1991). Both leaf margin features are regarded as apomorphic and strongly link *Sparaxis* to the *Tritonia* group, especially because morphology is equivocal concerning relationships in most Ixioideae. *Ixia*, thought to be allied to *Sparaxis* (Lewis, 1962; Goldblatt, 1969), has the plesiomorphic leaf margin anatomy, with the epidermis no different on margin and lamina, and well-developed subepidermal sclerenchyma associated with a marginal vein.

INFLORESCENCE AND BRACTS

There is nothing remarkable about the inflorescence of *Sparaxis*, a spike, but the patterns of branching are variable. In most members of section *Sparaxis* branching is restricted to the base, although plants may produce up to five axes per corm and this seems to be the basic condition in the genus. In *S. bulbifera* and section *Synnotia*, branching, when it occurs, is cauline, presumably a reversal to the basic kind of branching in Iridaceae including the possible outgroups of the genus. Flowers are more or less spirally arranged on a flexuose axis in section *Sparaxis*, but the spike is secund in those species with a zygomorphic perianth (sect. *Synnotia*). The two characters may be correlated, but are here regarded as separate synapomorphies.

The bracts of *Sparaxis* are perhaps the most striking feature of the genus. They are dry and firm in texture, somewhat creased, and usually long-cusped (Fig. 1). In addition, they are irregularly streaked with medium to dark brown on the pale translucent background. The bracts are remarkably similar to those of *Dierama*, which is presumed to be convergent. Bracts of *Ixia* and *Tritonia* are typically membranous and uniformly pale or with the veins a darker color, and in both genera the bracts are most often short-cusped. Three species of section *Sparaxis* stand out in having especially large but non-cusped bracts. Instead, the margins are rather irregularly lobed. This condition is assumed here to be the plesiomorphic state. In *S. fragrans* and *S. maculosa* the margins of the bracts including the cusps are irregularly fringed (Fig. 1A). The condition is distinctive enough to make it possible to identify the species from the bracts alone and must be regarded as apomorphic.

PERIANTH

The somewhat fleshy perianth is actinomorphic in section *Sparaxis*, but is medianly zygomorphic (Figs. 2, 3), a derived condition, in section *Synnotia*, in which the flowers face to the side, the upper tepal is always largest, and the lower three tepals are typically smaller, united to one another for a short distance, and grooved proximally. All members of section *Sparaxis* have a fairly short perianth tube, as do several of section *Synnotia*. An elongate tube characterizes *S. roxburghii* and the two subspecies of *S. variegata*, and in the latter the tube is bent sharply (geniculate) at the top of the lower cylindric part of the tube (Fig. 3B).

Floral variation in section *Sparaxis* is limited. All seven species have a regular perianth, and five have actinomorphic flowers with erect stamens symmetrically oriented around the central style. Two species have asymmetrically arranged stamens, described below.

In the flowers of section *Synnotia* the tepals are unequal, the adaxial tepal being largest and the lower three small, united for a short distance, and grooved. The stamens are unilateral and more or less contiguous, lying close to the posterior tepal.

Perianth colors of red to orange or pink, found in *Sparaxis tricolor*, *S. elegans*, and *S. pillansii*, are probably plesiomorphic, corresponding as they do to the predominant perianth colors in *Tritonia* and *Ixia*. The remaining species of *Sparaxis* have yellow to white or purple perianths.

I have not included floral odor in this analysis because the scents in the three fragrant species, *S. fragrans*, *S. caryophyllacea*, and *S. galeata*, seem different, and thus poor evidence for relationship. Moreover, based on all other criteria, the three scented species do not seem to be immediately related.

FIGURE 1. Habit and floral details of *Sparaxis maculosa* (A) and *S. bulbifera* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by J. C. Manning and M. L. Branch.)

STAMENS AND STYLE

Whereas in most species of section *Sparaxis* the stamens are arranged symmetrically around the central style, in *S. grandiflora* and *S. bulbifera* the stamens and style are asymmetrically arranged. The lower (abaxial) stamen is curved across the flower to lie opposite the upper (adaxial) tepal, and the style lies between this stamen and the posterior tepal (Fig. 1B). This condition is probably a step

FIGURE 2. Habit and floral details of *Sparaxis villosa* (A) and *S. caryophyllacea* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by M. L. Branch.)

toward the arched unilateral and more or less contiguous stamens of section *Synnotia* (Figs. 2, 3). In *S. grandiflora* and *S. bulbifera* and section *Synnotia* the anthers face inward and are introrse at anthesis, unlike the other species of section *Sparaxis*, which have extrorse anthers, the basal condition for Iridaceae. In *S. pillansii* the anthers are slightly coiled (S-shaped), and in *S. elegans* they are strongly twisted around the style (Goldblatt, 1969).

Three species of section *Sparaxis*, *S. tricolor*, *S. elegans*, and *S. pillansii*, have short, terminally expanded style branches, different from the filiform, relatively long style branches that characterize the rest of the genus (Goldblatt, 1969). Comparison with *Tritonia* suggests that the long filiform style branches are the basal condition and that the short branches are derived. A similar interpretation seems reasonable with *Ixia* as outgroup.

POLLEN

The pollen grains of several species examined are sulcate with a 2-banded operculum, and the exine has a perforate and minutely verrucate tectum (Goldblatt et al., 1991). In all these features the grains correspond fairly closely to the presumed basal condition in Ixioideae, although contrasting with *Ixia*, which has unusually small grains with a single banded operculum.

FRUIT AND SEEDS

The thin-walled capsules are unremarkable in Ixioideae and are more or less barrel-shaped to

FIGURE 3. Habit and floral details of *Sparaxis variegata* subsp. *variegata* (A) and subsp. *metelerkampiae* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by M. L. Branch.)

subglobose, but 3-lobed when seen from above. The translucent membranous walls of the ripe capsules show clearly the rounded impression of the seeds, a consequence of seed shape and texture rather than of any intrinsic feature of the capsule itself. The seeds of both sections *Sparaxis* and *Synnotia* are spherical, hard, and shiny. The raphe remains conspicuous, and there is a slight swelling around the micropyle. Color is medium brown to deep red-brown. Seed number is remarkably constant in a species, with an average of 8–10 seeds per locule (24–30 per capsule). Fewer seeds are found in *S. parviflora* (4–6 per locule) and *S. galeata* (2–4 per locule) and *S. variegata* subsp. *variegata* (5–6 per locule), while subspecies *metelerkampiae* has capsules with a greater number of seeds than the average (10–12 per locule). Size varies a little between the species, but the large seeds of *S. parviflora*, up to 2.5 mm diam., are clearly apomorphic. The small seeds of *S. variegata* subsp. *metelerkampiae*, 1.6–1.8 mm diam., are probably also apomorphic. Curiously, the above two taxa, one with many small seeds and the other with few large seeds are also the most strongly self-compatible and autogamous species in the genus.

KARYOLOGY

Basic chromosome number in *Sparaxis* is $x = 10$ (Goldblatt, 1969, 1971). The chromosomes are

small and exhibit a small range in size. Original counts here for two species of section *Synnotia*, *S. caryphyllacea* and *S. variegata* subsp. *metelerkampiae*, both $2n = 20$, conform to the pattern already described for the genus. This karyotype accords closely with that of *Ixia* and *Dierama*. *Tritonia* and *Crocosmia* have $x = 11$, but otherwise have a similar chromosome morphology. It is only a small change from $x = 11$ to $x = 10$, and there is ample precedent for single-step decreasing dysploid events in flowering plants, including several within Iridaceae.

Phylogeny of *Sparaxis*

The characteristics outlined above and summarized in Table 1 form the basis for the cladistic analysis. Characters were initially polarized using both *Ixia* and *Tritonia* as the outgroup. A more parsimonious resolution was obtained with *Tritonia*. The use of *Ixia* as outgroup is founded largely on karyotypic similarity, and the resulting cladogram thus assumes the convergent development of the two evidently unlinked and striking leaf anatomical characters, columnar marginal epidermal cells, and lack of subepidermal epidermis at the margins in *Sparaxis* and in the *Tritonia* lineage. I prefer to assume that a single decreasing dysploid event occurred in the *Sparaxis* line, resulting in the apparently identical karyotypes of *Ixia* and *Sparaxis*. The cladogram (Fig. 4) was produced by hand and verified using Hennig86. The computer analysis produced three trees of equal length, the one figured, a second that is not supported by the data, and a third that is discussed below, that have a tree length of 31 and a consistency index (CI) of 0.77, ignoring non-informative characters for the ingroup. Ignorance of seed type (character 25) in *S. roxburghii* and *S. variegata* makes it impossible to resolve completely the *Synnotia* clade. Depending on the character state for these two species a shorter tree length of 30 and CI of 0.8 can be obtained (as is figured), assuming many small seeds for *S. variegata* and few large seeds for *S. roxburghii*.

The most significant point of difference between the three computer-generated trees is the position of *Sparaxis parviflora*. Its position as sister clade to the remaining species of section *Synnotia* (Fig. 4) where it is defined by two parallelisms is the one I prefer. But in one tree *S. parviflora* is the sister clade to *S. galeata–S. roxburghii*, and the cluster is supported by the presumed presence of few large seeds (character 25). Ignorance of the seeds of *S. roxburghii* renders informed comment on the tree impossible.

A notable parallelism in the tree is the elongate perianth tube in *S. roxburghii* and *S. variegata*, species which have different types of corms. A longer tree results when these two species are treated as related by their long tubes, for there is then a reversal in corm tunic texture and two parallelisms, one for an erect upper tepal and another for tunics thick and forming a neck. Other parallelisms in the tree, including a small flower in *S. parviflora* and *S. villosa*, spotted leaf bases in *S. galeata* and *S. caryophyllacea*, and few and large seeds in *S. parviflora* and *S. galeata*, are not unusual for plants in general. The presence of cauline branching for the clade including the *Synnotia* group and *S. bulbifera* is treated as a reversal, basal branching being regarded here as apomorphic for *Sparaxis*. The reversal of one of the basal characters for *Sparaxis*, oblique apiculate leaf apices, in *S. fragrans* is not surprising in view of its narrow leaves, which leave little opportunity for the expression of the character.

The analysis confirms the integrity of *Synnotia* as a monophyletic assemblage. The *Synnotia* clade is supported by three synapomorphies, all related to floral zygomorphy and thus perhaps intimately linked. The analysis also indicates that while the genus *Sparaxis* is monophyletic and is supported by five synapomorphies, none evidently linked, the seven species of *Sparaxis* sensu Goldblatt (1969), i.e., excluding *Synnotia*, do not themselves constitute a single lineage, but rather consist of four clades, more or less equivalent to the *Synnotia* clade.

Treatment of these seven species as a section *Sparaxis* is taxonomically convenient, although phylogenetically unacceptable because section *Sparaxis* as so constituted is paraphyletic. The recommended phylogenetic solution, to recognize these seven species as four sections equivalent to section *Synnotia* (or no sections at all) has little practical merit. Excepting the basal clade that includes *S. tricolor* and its two relatives, the lineages are supported by only one synapomorphy each. On grounds of taxonomic utility, I suggest treating *Sparaxis* as two sections, section *Synnotia* and a residual and paraphyletic section *Sparaxis*. It must be noted that within the latter, the *S. tricolor* line stands out from the remaining four species, which though constituting three primary clades, are in fact so closely related that they are in practice often difficult to distinguish, and their validity as separate species has not always been accepted (e.g., Lewis, 1950). Recognition of a third section *Tri-*

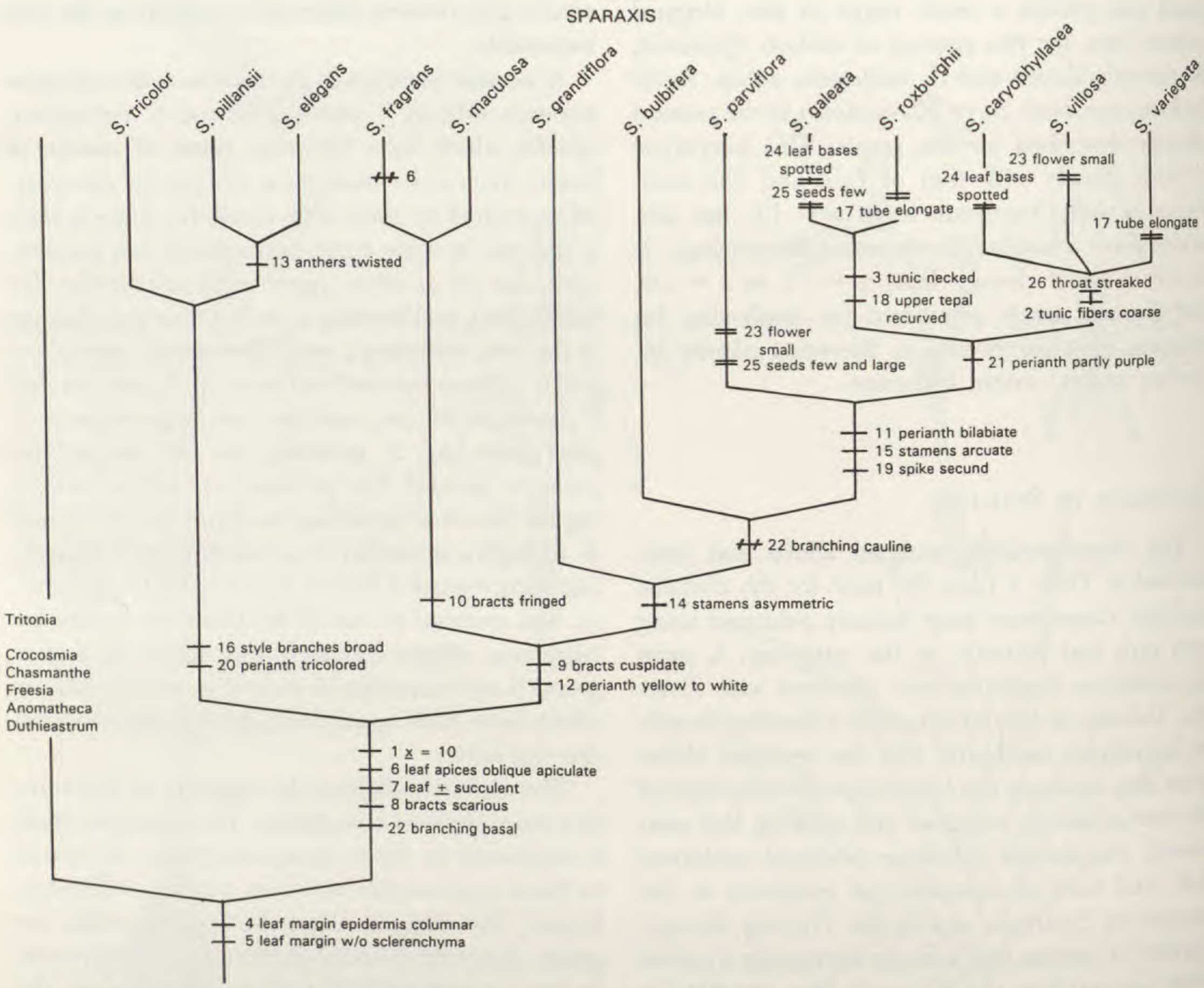

FIGURE 4. Phylogeny of *Sparaxis*, with *Tritonia* and its close allies (*Crocosmia, Chasmanthe, Freesia,* and *Anomatheca*) as outgroup. The cladogram is based on the character list and data matrix presented in Table 1. Tree length is 30 and the consistency index (CI) is 0.8, with autapomorphies excluded for the manually constructed cladogram. Parallelisms are indicated by double lines and reversals by barred lines.

color has merit, but because of its small size formal treatment seems unnecessary at present.

SYSTEMATIC REVIEW

The species of *Sparaxis* are dealt with briefly below in taxonomic sequence. Because full descriptions are provided in a treatment of the genus for *Flora of Southern Africa* (Goldblatt, in press) they are not repeated here. Only brief synonymy is given except where new combinations are presented. Extended descriptions are provided for two new species, *S. maculosa* and *S. caryophyllacea* and for *S. variegata*, which has a complex pattern of variation. Complete species descriptions and ample citation of specimens are included in revisions of *Synnotia* (Lewis, 1956) and *Sparaxis* in part (Goldblatt, 1969). I have not included sectional descriptions here because they have little utility in a small genus like *Sparaxis* and would call for near repetition of the generic description except for the fact that the section *Sparaxis* has an actinomorphic perianth and section *Synnotia* has a zygomorphic one.

Sparaxis Ker, Curtis's Bot. Mag. 15: t. 548. 1802, & Konig & Sims, Ann. Bot. 1: 225. 1804 as 1805. Klatt, Linnaea 32: 747. 1863, & Abh. Naturf. Ges. Halle 15: 389 (Erganz. 56). 1882, not including *Synnotia* or *Streptanthera*. Baker, Handb. Irid. 196. 1892, & in Flora Cap. 6: 115. 1896, not including *Synnotia* or *Streptanthera*. Goldblatt in J. S. African Bot. 35: 219–252. 1969, not including *Synnotia*; Contr. Bolus Herb 13: 57. 1991. TYPE SPECIES: *S. bulbifera* (L.) Ker (lectotype, here designated).

Streptanthera Sweet, Brit. Fl. Gard. ser. 1, 3: t. 209. 1827, Klatt, Abh. Naturf. Ges. Halle 15: 390 (Erganz. 56). 1882. Baker, Handbk. Irid. 160 (1892) & in Flora Cap. 6: 86. 1896. E. Phillips, Gen. S.

TABLE 1. Data matrix and character list for the cladogram (Fig. 4). The derived condition is denoted by 1; ancestral by 0; state unknown by ?. Polarity of characters is discussed in the text. Autapomorphies are not included. Abbreviations for species will be evident from the text and Figure 4.

	Character number																									
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Tritonia	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sparaxis																										
tric.	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
eleg.	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
pill.	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
frag.	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
macu.	?	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	?	0
grand.	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
bulb.	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
parvi.	?	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	1	0	1	0
gale.	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	1	1	0
roxb.	?	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	0	0	0	?	0
vill.	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	0	1	0	1	0	0	1
caryo.	1	1	0	1	1	1	1	1	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1
varie.	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	?	1

Characters: the derived (apomorphic) states listed first followed by the presumed ancestral (plesiomorphic) condition.

1. basic chromosome number $x = 10$—$x = 11$
2. corm tunics of coarse fibers thickened below—tunics fibers fine
3. corm tunics forming a neck and accumulating in a dense mass—tunics not forming a neck nor a dense mass
4. leaf margin epidermis columnar—epidermis normal
5. margins without subepidermal sclerenchyma—subepidermal sclerenchyma present
6. leaf apices obtuse and oblique apiculate—apices acute
7. leaves ± succulent and gold-reflecting—leaves firm, not gold-reflecting
8. bracts scarious, creased and brown streaked—bracts membranous and self-colored
9. bracts long-cuspidate and lacerate—bracts not cuspidate or hardly scarious
10. bract edges irregularly serrate-fringed—bract edges smooth
11. perianth zygomorphic and bilabiate—perianth actinomorphic
12. perianth shades of yellow to white or purple—perianth with red, orange or pink
13. anthers weakly twisted—anthers straight
14. abaxial stamen opposed to adaxial tepal and style arcuate—stamens and style symmetrically arranged
15. stamens unilateral and arcuate—stamens not unilateral
16. style branches short and broad above—style branches filiform
17. perianth tube elongate—perianth tube short
18. upper tepal erect-recurved—upper tepal hooded
19. spike secund—spike spiral
20. perianth vividly marked (tricolored)—perianth usually drably marked (uni- or bicolored)
21. perianth with at least upper tepal partly purple—perianth without purple marks
22. branching basal only—branching cauline
23. flowers especially small—flowers fairly large
24. leaf bases spotted—leaf bases self-colored
25. seeds few and large—seeds many and moderate-sized
26. perianth throat streaked—throat not streaked

Afr. Fl. Pl. ed. 2: 218. 1951. TYPE SPECIES: *S. elegans* Sweet (= *Sparaxis elegans* (Sweet) Goldblatt).

Synnotia Sweet, Brit. Fl. Gard. 2: t. 150. 1826 (as *Synnetia*), corr. *Synnotia* by Sweet in Hort. Brit. ed. 2: 501. 1827. Klatt, Linnaea 32: 750. 1863. Baker, Flora Cap. 6: 134–135. 1896. Lewis, Ann. S. African Mus. 40: 137–151. 1956. TYPE SPECIES: *S. variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt).

Anactorion Raf., Fl. Telluriana 34. 1838 (as 1836). TYPE: *A. bicolor* (Thunb.) Raf. (= *Sparaxis villosa* (Burm. f.) N. E. Br.).

Geophytic perennials with small globose corms rooting from the base; *corm tunics* of fine to moderately fine netted fibers or of coarse hard fibers, thickened and clawlike below. *Leaves* several, mostly basal, but sometimes also cauline, the lowermost 2–3 membranous and sheathing (thus cataphylls), the remaining laminate and green, lanceolate to linear or falcate, obtuse to acute, acuminate, often obliquely so, glabrous, with many closely set fine secondary veins, the midrib prominent. *Stem* firm and relatively thick, ± erect, glabrous, simple

or branched, then either from near the base or above the ground, sometimes with a few large axillary cormlets below, or many small cormlets in all axils. *Spike* (1–)few- to several-flowered, lax, distichous in bud, loosely spiral or nearly secund in bloom; *bracts* scarious and creased, pale with brown streaks, ± entire to lightly lacerate, or deeply lacerate with long tapering cusps, the outer (abaxial) larger than the inner (adaxial). *Flowers* actinomorphic or zygomorphic, then with either the stamens alone asymmetrically arranged or the perianth also asymmetric, then the upper (adaxial) tepal larger and often hooded and the lower three tepals smallest, with contrasting marking and extended forward ± horizontally; *perianth tube* short to long, funnel-shaped (cylindric below and expanded above), sometimes obliquely so, or elongate, much exceeding the bracts and dimorphic, the lower part cylindric and abruptly bent and widened above; *tepals* with the whorls ± equal or the upper largest and the lower three smallest, lanceolate to obovate or spathulate, acute to obtuse. *Stamens* inserted at the base of the expanded part (throat) of the tube, symmetrically or asymmetrically disposed; *filaments* filiform, straight and surrounding the style, or curved outwards and the abaxial twisted to lie opposite the adaxial tepal, or all three filaments ± parallel and opposite the adaxial tepal; *anthers* straight, curved or spirally coiled, subbasifixed, extrorse or introrse. *Ovary* ovoid; *style* filiform, straight and erect or unilateral, the branches either short, often with expanded apices, or long and filiform. *Capsules* barrel-shaped to oblong, firm-membranous, showing the outline of the seeds; *seeds* (2–)4–15 per locule, globose, relatively large, smooth, usually shiny. *Chromosome number* $x = 10$.

A genus of 13 species, all in South Africa and restricted to the southwestern Cape, southern Namaqualand, and the western Karoo.

Key to the Species

1a. Perianth actinomorphic; stamens either symmetrically disposed around a central style or the abaxial stamen lying opposite the adaxial tepal, and style opposite the adaxial tepal (section *Sparaxis*).
  2a. Bracts entire to slightly lacerate; stamens symmetrically disposed around erect style (this includes when anthers are coiled).
    3a. Anthers spirally coiled and reaching only to apex of the style ..... 3. *S. elegans*
    3b. Anthers straight or slightly twisted and curved, extending well past style branches.
      4a. Anthers straight, yellow to ochre; spikes 2–5-flowered; tepals orange, marked with yellow and black ..... 1. *S. tricolor*
      4b. Anthers incurved and slightly twisted, red to brown; spikes (2–)5–10-flowered; tepals rose pink, marked with yellow and red to purple ..... 2. *S. pillansii*
  2b. Bracts deeply lacerate with cusps at least as long as the rest of the bract; stamens symmetrical or asymmetrical but not coiled.
    5a. Bract edges irregularly serrate (fringed); stamens symmetrically arranged around style.
      6a. Tepals 27–35 × 8–10 mm; leaves oblong to lanceolate, 9–12 mm wide and obliquely apiculate ..... 5. *S. maculosa*
      6b. Tepals 18–25 × 5–8 mm; leaves linear to narrowly lanceolate, 2–5(–9) mm wide and acute ..... 4. *S. fragrans*
    5b. Bract edges ± entire, not serrate or fringed; stamens asymmetrically disposed.
      7a. Stem usually branched in mid-axis and bearing a cauline leaf; many small cormlets produced after flowering at all nodes ..... 7. *S. bulbifera*
      7b. Branches if present produced from base, and axes lacking a cauline leaf; cormlets not produced in numbers and never above ground ..... 6. *S. grandiflora*
1b. Perianth zygomorphic, with the adaxial (upper) tepal largest, erect, and often hooded, and lower three tepals smallest and ± horizontal; stamens unilateral and arcuate, with the anthers parallel and ± contiguous (section *Synnotia*).
  8a. Narrow part of perianth tube more than 25 mm long, well exserted from the bracts; tube bent abruptly (geniculate) at apex of the slender part ..... 13. *S. variegata*
  8b. Narrow part of perianth tube less than 25 mm long, exserted or included in the bracts; tube gently to sharply curved at the apex of the narrow part.
    9a. Corm tunics of fine fibers; flowers small, the tepals less than 10 mm long ..... 8. *S. parviflora*
    9b. Corm tunics either of fine or coarse fibers thickened into claws below; flowers usually larger, the upper tepals at least 15 mm long, but if shorter the corm tunics of coarse fibers.
      10a. Corm tunics of hard reticulate fibers not extending upwards in a neck; upper tepal directed forward and somewhat hooded over the stamens.
        11a. Upper tepal ca. 16 mm long, bases of the leaves uniformly colored; style dividing opposite the lower half of the anthers, the style branches ca. 2 mm long ..... 11. *S. villosa*
        11b. Upper tepal 22–24 mm long; bases of the leaves lightly speckled with purple (not

visible in dry material); style dividing near anther apices, the style branches ca. 5 mm long ..... 12. *S. caryophyllacea*

10b. Corm tunics of fine fibers, usually extending upwards in a neck; upper tepal erect or directed backwards.

12a. Cylindrical part of perianth tube less than 8 mm long; leaf bases spotted red to purple (sometimes fading on dry specimens) ..... 9. *S. galeata*

12b. Cylindrical part of perianth tube 15–25 mm long; leaf bases uniformly colored ..... 10. *S. roxburghii*

SECTION 1. *SPARAXIS*

1. **Sparaxis tricolor** (Schneev.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 117. 1896. Goldblatt, J. S. African Bot. 35: 230. 1969. *Ixia tricolor* Schneev., Icon. Pl. Rar. t. 39. 1795. Ker, Curtis's Bot. Mag. 11: t. 381. 1797. *Streptanthera tricolor* (Schneev.) Klatt, Abh. Naturf. Ges. Halle 15: 390 (Erganz. 56). 1882. TYPE: illustration in Schneevogt, Icon. Pl. Rar. t. 39.

Restricted to the northern end of the Bokkeveld Escarpment, northwest of Nieuwoudtville in the northwestern Cape, occurring on clay soils in renosterveld. Readily identified by the characteristic orange-red flowers with yellow and blackish tepal markings. Widely cultivated in southern Africa and elsewhere; most *Sparaxis* hybrids were derived from crosses that included *S. tricolor*.

2. **Sparaxis pillansii** L. Bolus, S. African Gard. 22: 57. 1932. Goldblatt, J. S. African Bot. 35: 232. 1969 & Ann. Missouri Bot. Gard. 68: 563. 1981. TYPE: South Africa. Cape: near Nieuwoudtville, *L. Bolus s.n.* (holotype, BOL-19182).

Endemic to the Calvinia District in the northwestern Cape, it is most common in the rocky hills east of Nieuwoudtville but is also found near Calvinia. Occurring in heavy red clay waterlogged for most of the growing season, often in standing pools. Closely related to *S. tricolor*, and with flowers having similar, though smaller markings, *S. pillansii* is easily distinguished by differences in tepal coloring (orange and blackish in *S. tricolor*, rose and reddish in *S. pillansii*), and by its weakly twisted anthers.

3. **Sparaxis elegans** (Sweet) Goldblatt, J. S. African Bot. 35: 233. 1969. *Streptanthera elegans* Sweet, Brit. Fl. Gard. ser. 1, 3: t. 209. 1827. Baker, Flora Cap. 6: 86. 1896. TYPE: figure in Brit. Fl. Gard. ser. 1, 3: t. 209.

Streptanthera cuprea Sweet, Brit. Fl. Gard. ser. 2, 2: t. 122. 1831 (Sweet, Hort. Brit. ed. 2: 501. 1830, nom. nud.). Baker, Flora Cap. 6: 86. 1896. Polevans in Fl. Pl. South Africa 8: pl. 320. 1928. *Sparaxis cuprea* (Sweet) Klatt, Linnaea 35: 378. 1868. TYPE: figure in Brit. Fl. Gard. ser. 2, 2: t. 122.

Streptanthera cuprea var. *non-picta* L. Bolus, S. African Gard. 22: 276. 1932. Marais, Curtis's Bot. Mag. 177: t. 557. 1969. TYPE: South Africa. Cape: Nieuwoudtville, *Buhr s.n.* (holotype, BOL 19443).

Endemic to the Bokkeveld Plateau in the northwest Cape, extending from about Nieuwoudtville southward some 25 km; occurring in light to heavy clay soils. Easily recognized by the distinctively marked flowers, the coiled anthers twisted around the style and the unusually broad style branches. The more common form with salmon-pink flowers occurs in the Nieuwoudtville area, and the white-flowered form occurs in the south of its range, sometimes in pure stands, or mixed with the pink.

4. **Sparaxis fragrans** (Jacq.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 117. 1896. Goldblatt, J. S. African Bot. 35: 235. 1969. *Ixia fragrans* Jacq., Icon. Pl. Rar. 2: t. 274. 1793. TYPE: figure in Jacquin, Icon. Pl. Rar. 2: t. 274.

Ixia sordida Hornem., Hort. Hafn. Suppl. 6. 1819. TYPE: South Africa, without precise locality, *Hornemann s.n.* (holotype, C).

Gladiolus odorus Schrank, Denkschr. Königl.-Baier Bot. Ges. Regensburg 2: 206. 1822, nom. illeg. non Salisb. (1796) nec *Gladiolus fragrans* Jacq. (1797). Type as for *Ixia fragrans* Jacq.

Endemic to the Caledon District in the southwestern Cape, extending from Botrivier and Villiersdorp in the west to the east end of the Caledon Swartberg in the east; occurring on clay flats and slopes, usually waterlogged in the winter months. Distinguished by the small yellow to buff, unpleasantly scented flowers with symmetrically disposed stamens and narrowly acute leaves. Closely related to *S. maculosa* (below) which has similar fringed to serrate bract margins.

5. **Sparaxis maculosa** Goldblatt, sp. nov. TYPE: South Africa. Cape: farm Stettyn, between Worcester and Villiersdorp, *Perry & Manning 3603* (holotype, NBG; isotypes, K, MO, PRE). Figure 1A.

Plantae 10–20(–30) mm altae, cormo globoso ca. 15. cm diam., foliis 7–9, lanceolatis, 9–12 mm latis, spica 1–2(–3)-flora, bracteis scariosis laceratis cuspidatis, floribus actinomorphis stellatis, flavis in medio atromarroninis, filamentis erectis, antheris ascendentibus 9.5–11 mm longis, ramis stylorum inter antheris recurventibus.

Plants 10–20(–30) cm high. *Corm* globose, ca. 1.5 cm diam., tunics of fine, pale, closely matted fibers. *Foliage leaves* 7–9, all ± basal, about 2/3 as long as the spikes, the upper longest, lanceolate(–oblong), 9–12 mm wide, abruptly expanded adaxially above the sheath, obtuse, obliquely apiculate. *Stem* nearly erect, flexed above the first flower, leafless above the ground, simple or with 1–2 branches produced from below ground level. *Spike* 1–2(–3)-flowered, weakly flexuose; *bracts* scarious, translucent with light brown streaks toward the margins, the outer 3-cuspidate, the inner 2-cuspidate, both lacerate, and the edges lightly and irregularly serrate, 2–2.5 mm long, the cusps slightly exceeding the rest of the bract. *Flowers* actinomorphic, stellate, bright yellow, the tepals each with a dark maroon heart-shaped mark with a central yellow streak in the lower third; *perianth tube* funnel-shaped, 6–7 mm long, the lower part ca. 2.5 mm long; *tepals* ± oblong, 27–35 mm long, 8–10 mm wide. *Filaments* 6–7 mm long, erect, contiguous around the style; *anthers* linear, 9.5–11 mm long, pale yellow. *Ovary* globose, ca. 2.5 mm long, *style* filiform, dividing opposite the lower third of the anthers, branches 4.5–5 mm long, arching between the upper anthers. *Capsules* and *seeds* unknown. *Chromosome number* unknown.

Discovered in 1988, *Sparaxis maculosa* is known only from the farm Stettyn, north of Villiersdorp, in the Worcester valley. It grows on clay soils in seasonally waterlogged conditions and blooms in September. It is closely related to *S. fragrans*, and the basic form of their actinomorphic flowers is identical. Their bracts are also similar, being long-cuspidate and irregularly lacerate with the edges lightly and irregularly serrate (or somewhat fringed), a feature that alone makes it possible to identify the two species.

As circumscribed by Goldblatt (1969), *Sparaxis fragrans* includes slender plants with linear to narrowly lanceolate (or falcate), acute leaves 2–8 mm wide and a spike of 1–3(–5) scented, pale yellow to buff flowers. The tepals are uniformly narrow, the stamens symmetrically disposed with the filaments contiguous and surrounding the lower part of the style, and the anthers divergent. The style branches are relatively long and curve outwards over and between the anthers. Occasionally the flowers have a small single or paired dark mark at the base of each tepal, while the outer or both whorls of tepals may be flushed with purple on the reverse. Unlike *S. fragrans*, the leaves of *S. maculosa* are short, oblong to lanceolate, and obtuse and obliquely apiculate, and the stems have one or rarely two flowers, which are larger than any known in *S. fragrans*, although the perianth tube is about the same length in both. In *S. maculosa* the clear, bright yellow tepals each have a large heart-shaped, dark maroon mark in the lower third.

The single known population is relatively small but quite uniform for these characters. The question arises whether it is simply a divergent population of *S. fragrans*, or whether it is sufficiently distinct to merit taxonomic recognition. Comparison with variation patterns among taxa within *Sparaxis* suggests that the differences in the leaves alone would merit taxonomic separation at subspecific rank. Less pronounced leaf differences exist in *S. grandiflora* between subspecies *grandiflora* and subspecies *violacea*, which are also separated by small differences in tepal shape (Goldblatt, 1969, in press). The substantial leaf and floral differences including tepal width, length, and patterning, style arm length, and level of division relative to the anthers make it seem preferable to accord the Stettyn population recognition at the species rank. The distinction in leaf shape, tepal size, and relative proportion of other floral characters are absolute. There is no overlap in any floral or leaf characters. Additional exploration in suitable sites in the southern Worcester valley may yield further populations that render this decision liable to revision, but until then specific rank for the population seems preferable.

6. Sparaxis grandiflora (Delaroche) Ker, König & Sims Ann. Bot. 1: 225. 1804 (Sept.–Nov.) & Curtis's Bot. Mag. 20: t. 779. 1804 (Oct.). Baker, Flora Cap. 6: 116. 1896. G. Lewis, Fl. Cape Penins. 245. 1950, in part including *S. bulbifera*. Goldblatt, J. S. African Bot. 35: 239. 1969. *Ixia grandiflora* Delaroche, Descr. Pl. Nov. 23. 1766. Ker, Curtis's Bot. Mag. 15: t. 541. 1801. TYPE: South Africa. Cape: near Tulbagh Road Station, *Goldblatt 303* (neotype, designated by Goldblatt (1969), BOL; isoneotype, MO).

Ixia uniflora L., Mant. 27. 1770. TYPE: without precise locality, Herb. Linnaeus 58/19 (holotype, LINN).

Widespread in the southwestern Cape from Clanwilliam in the northwest to Breadasdorp in the southeast, occurring on heavy clay soils, often wa-

terlogged in the winter; flowering August to September. The species is variable, and four allopatric subspecies were recognized by Goldblatt (1969). Although finely drawn, each seems to represent a separate race of the species, geographically isolated from the others by mountain and soil barriers. The subspecies will be fully treated in the *Flora of Southern Africa* treatment (Goldblatt, in press), which will include the extensive and complex synonymy, key, and descriptions.

Subspecies *grandiflora*, with plum-colored flowers, is restricted to the Tulbagh valley; subspecies *fimbriata*, with cream flowers, occurs along the western Cape coastal plain; subspecies *violacea*, which has either purple or white flowers, in the Caledon district, east of the Houw Hoek Mountains; and subspecies *acutiloba*, with yellow (rarely violet) flowers, occurs to the north, in the Olifants River valley.

7. **Sparaxis bulbifera** (L.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 116. 1896, in part excl. *S. grandiflora* subsp. *violacea* as variety B, *violacea*. Goldblatt, J. S. African Bot. 35: 236. 1969. *Ixia bulbiflera* L., Amoen. Acad. 300. 1756. *Belamcanda bulbifera* (L.) Moench (as *Belemcanda*), Suppl. Meth. 214. 1802. TYPE: without precise locality, Herb. Linnaeus 58/16 (neotype, designated by Goldblatt (1969), LINN). Figure 1B.

Ixia anemonaeflora sensu DC. in Redouté, Liliac. 2: t. 85. ca. 1804, non Jacq. (1793) (= *Ixia campanulata* Houtt.).

Sparaxis albiflora Ecklon, Topogr. Verz. 28. 1827. TYPE: cited as *Zeyher s.n.* (isotype, SAM) by Goldblatt (1969), but uncertain.

Widespread in the southwestern Cape, extending from Darling in the west to Bredasdorp in the east, occurring on flats and lower slopes of hills and mountains, and mostly in sandy ground, waterlogged in winter, occasionally on wet clay soils. Often confused with white-flowered forms of *Sparaxis grandiflora* and sometimes distinguished only with difficulty in early flower by its taller stature and preference for wet, sandy habitats; identification is easier after the aerial branch and small axillary cormlets develop.

SECTION 2. *SYNNOTIA*

Sparaxis sect. **Synnotia** (Sweet) Goldblatt, Contr. Bolus Herb. 14: 57 (1991). *Synnotia* Sweet, Brit. Fl. Gard. 2: t. 150. 1826 (as *Synnetia*), corr. *Synnotia* by Sweet in Hort. Brit. ed. 2: 501. 1827. TYPE SPECIES: *S. variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt subsp. *variegata*).

8. **Sparaxis parviflora** (G. Lewis) Goldblatt, comb. nov. Basionym: *Synnotia parviflora* G. Lewis, Ann. S. African Mus. 40: 140–142. 1956. TYPE: South Africa. Cape: between Darling and Mamre, *Lewis 3556* (holotype, SAM 65637; isotype, K).

Restricted to the coastal plain between Cape Town and Saldanha Bay and occurring in sandy, granite-derived soils, often in rock outcrops, where it flowers fairly early in the season, beginning in mid-August. Easily recognized by its tiny cream and pale yellow flowers, the smallest in the genus, and the finely fibrous corm tunics, *Sparaxis parviflora* is a strongly autogamous species. The seeds are the largest in the genus.

A form of *S. villosa* with unusually small flowers can be distinguished from *S. parviflora* by its thickened and clawed corm tunics and flowers with the upper tepals flushed with purple.

9. **Sparaxis galeata** Ker, König & Sims, Ann. Bot. 1: 225–226. 1804, as nom. nov. pro *Gladiolus galeatus* Jacq., Icones Pl. Rar. 2: t. 258. 1794 et Coll. Bot. 4: 167. 1792 (as 1790), nom. illeg. non *G. galeatus* Burman f. 1768 (= *Gladiolus alatus* L.). *Synnotia galeata* (Ker) Sweet, Hort. Brit. ed. 1, 398. 1827. Pole Evans, Fl. Pl. Africa 5: pl. 162. 1925 (as *Synnotia villosa*). Lewis, Ann. S. African Mus. 40: 143–146. 1956. *Anactorion galeatum* Raf., Fl. Telluriana 4: 34. 1838 (as 1836). TYPE: illustration in Jacq., Icones Pl. Rar. 2: t. 258.

Restricted to the lower Olifants River valley more or less between Clanwilliam and the foot of the Bokkeveld (Nieuwoudtville) Escarpment, *Sparaxis galeata* occurs on dry, arid, stony clay flats and gentle slopes. Unlike most species of *Sparaxis*, *S. galeata* is self-incompatible and it sets few, if any, seeds unless cross-pollinated. Seed set via deliberate or accidental selfing is infrequent. The unusually small capsules, 5–7 mm long, contain only 2–3(–4) seeds per locule. In addition to the capsules, it is easily distinguished by the corm tunics that accumulate in a dense mass and extend upwards to ground level in a neck, a character shared in *Sparaxis* only with *S. roxburghii*. The large, brightly colored and intensely fragrant, short-tubed flowers bloom from early August to mid-September.

10. Sparaxis roxburghii (Baker) Goldblatt, comb. nov. Basionym: *Synnotia bicolor* var. *roxburghii* Baker, Handbk. Irid. 198. 1892; Flora Cap. 6: 135. 1896. *Synnotia roxburghii* (Baker) G. Lewis, Ann. S. African Mus. 40: 146–147. 1956. TYPE: South Africa. Cape: 15 mi. N of Citrusdal, *Lewis 5207* (neotype, here designated, NBG; isoneotype, MO) (*Roxburgh s.n.*; the original type, without precise locality, has not been located).

Except for the type, from an unknown source, *Sparaxis roxburghii* has apparently been recorded from a single locality, a shale ridge near Alpha in the Olifants River valley between Citrusdal and Clanwilliam, flowering from late August to mid-September. It is rare and has not been collected for over 30 years. The species must be regarded as seriously endangered until its status can be assessed by on-site investigation. Its fine corm tunics that form a neck around the base and erect to reflexed, rather than hooded, upper tepal suggest that *S. roxburghii* is most closely related to *S. galeata*, but it can be distinguished immediately by its long perianth tube and differently colored and proportioned flower. Capsules and seeds of *S. roxburghii* are unknown.

11. Sparaxis villosa (Burman f.) Goldblatt, comb. nov. Basionym: *Gladiolus villosus* Burman f., Flora Cap. Prod. 2. 1768. *Synnotia villosa* (Burman f.) N. E. Br. Kew Bull. 133. 1929. Lewis, Ann. S. African Mus. 40: 142–143. 1956. TYPE: South Africa. Cape: without precise locality, illustration in Breyne, Prodr. Fasc. Rar. Pl., Icones 22: t. 8 f. 2. 1739 (lectotype effectively designated by Brown, 1929). Figure 2A.

Gladiolus bicolor Thunb., Diss. de Gladiolo no. 16, t. 2, f. 1. 1784. Jacquin, Ic. Pl. Rar. 2: t. 240. 1794. *Ixia bicolor* (Thunb.) Ker, Bot. Mag. 15: t. 548. 1802, nom. illeg. superfl. pro *Gladiolus villosus* Burman f. *Sparaxis bicolor* (Thunb.) Ker, König & Sims, Ann. Bot. 1: 225. 1805. *Synnotia bicolor* (Thunb.) Sweet, Hort. Brit. ed. 1: 398. 1827. Baker, Flora Cap. 6: 134–135. 1896, excl. syn. *Gladiolus galeatus* & var. *roxburghii*. *Anactorion bicolor* (Thunb.) Raf., Fl. Telluriana 4: 34. 1838 (as 1836). TYPE: South Africa. Cape: Groene Kloof, *Thunberg s.n.* (holotype, UPS).
(Figure 162 in Fl. Pl. Africa 5. 1925, identified as *Synnotia bicolor*, is *Sparaxis galeata*.)

The most widespread member of section *Synnotia*, *S. villosa* extends from the Cape Peninsula northward along the west coast and through the Tulbagh and Olifants River valleys as far north as Citrusdal. It occurs in renosterveld on heavy clay and granite-derived soils, often in rocky sites but also under low shrubs where it blooms more erratically than plants in open habitats. It flowers from late August to the end of September.

A small-flowered form in the Saldanha district can be confused with *S. parviflora*, but that species has corm tunics of fine-netted fibers unlike the coarse fibers with their clawlike thickenings characteristic of *S. villosa*.

12. Sparaxis caryophyllacea Goldblatt, sp. nov. TYPE: South Africa. Cape: middle slopes of the Nardouw Mountains, north of Clanwilliam, *Goldblatt 3851* (holotype, NBG; isotypes, K, MO, PRE). Figure 2B.

Plantae 12–30 cm altae, cormo 13–18 cm diam, spica 2–4-flora, floribus luteis, tepalo superiore violascente, faucibus atromaculatis, tubo perianthii ca. 20 mm longo, tepalo superiore ca. 20 mm longo erecto-arcuato, antheris ca. 4.5 mm longis.

Plants 12–30 cm high. *Corm* 13–18 cm diam., tunics of hard, coarse fibers oriented vertically, usually thickened below into clawlike ribs. *Foliage leaves* 5–7, basal except the upper 1–2, these inserted in the mid part of the stem, broadly lanceolate, 10–15 mm wide, usually obtuse, apiculate, sometimes obliquely so. *Stem* simple or with 1–2 branches produced in the axils of cauline leaves, usually inclined and slightly flexed above the leaves. *Spike* 2–4-flowered, straight or barely flexuose, ± secund; *outer bracts* pale below with whitish veins, becoming feathered light brown above, 12–14 mm long, lacerate, usually with a prominent central cusp, inner bracts similar, usually 2-cusped. *Flower* pale yellow with the upper tepal shading to violet in the upper half, the upper lateral tepals cream above the base, and the lower tepals deep yellow, fading to cream at the apices, the throat yellow with dark streaks, sweetly carnation-scented; *perianth tube* funnel-shaped, the upper part curving outward, ca. 20 mm long; *tepals* unequal, the upper largest and erect to slightly hooded, ca. 20 mm long, the upper laterals 16 mm long, directed forward, the lower tepals united for 3 mm, ± horizontal proximally, ca. 12 mm long, distally flexed downward and channeled. *Filaments* unilateral and arcuate, whitish, ca. 12 mm long; *anthers* white, ca. 4.5 mm long, only the upper parts exserted from the mouth of the tube; pollen cream. *Ovary* ca. 3.5 mm long, ovoid-trigonous; *style* arched behind the filaments, white, dividing just below the apices of the anthers, branches diverging and recurved in the upper half, spread above the

anthers, conduplicate below, becoming narrowly channeled toward the upper third and the margins sparsely ciliate in the wider upper half. *Capsule* rotund, 10–11 mm long, 6–7 mm at the widest; *seeds* 1.8–2.2 mm diam., middle brown, usually 10 per locule. *Chromosome number* $2n = 20$.

Apparently very localized, *Sparaxis caryophyllacea* is known only from the western slopes of the Nardouw Mountains in the Olifants River valley between Bulshoek and the confluence of the Doorn River near Trawal where it was first collected in 1976. It grows in stony clay, below the contact line with the lowermost band of Table Mountain Sandstone that caps the range. The large flowers are produced from early August to mid-September and are sweetly scented. *Sparaxis caryophyllacea* is self-compatible and sets full capsules, containing ca. 30 seeds, when hand-pollinated with its own pollen, and is sometimes autogamous in the greenhouse, presumably when the stigmatic surfaces of styles of wilting flowers come into contact with pollen. In nature the species is probably outcrossing and pollinated by bees.

The flowers most closely resemble those of *Sparaxis villosa* (Fig. 2A), and it is to this species that *S. caryophyllacea* is probably most closely related. It can be readily distinguished by size, the upper tepals ca. 20 mm long compared with 12–16 mm in *S. villosa*. In addition the perianth is conspicuously striped with black in the throat and is strongly carnation-scented. Another diagnostic feature is the red speckling on the sheaths of the lower leaves. This character is also present in *S. galeata*, presumably due to convergence, for the two do not seem immediately related. *Sparaxis caryophyllacea* would make a fine container or rock garden subject. It is as easy to grow as the *Sparaxis* hybrids available in the horticultural trade.

13. Sparaxis variegata (Sweet) Goldblatt, comb. nov. Basionym: *Synnotia variegata* Sweet, Brit. Fl. Gard. 2: t. 150. 1826. Baker, Flora Cap. 6: 135. 1896. Lewis, Ann. S. African Mus. 40: 147–149. 1956. TYPE: illustration in Brit. Fl. Gard. 2: t. 150. Figure 3.

A relatively common species of the western Cape interior, *S. variegata* extends from the upper Olifants River valley through the Cedarberg to the Nieuwoudtville escarpment, occurring on sandstone-derived soils or in sandstone outcrops; flowering mid-August through September. It stands out because of its corms with coarsely fibrous tunics and flowers with a long perianth tube with a strong geniculate bend at the apex of the slender, cylindric part of the tube (Fig. 3).

Lewis's (1956) treatment of this species as comprising two infraspecific taxa is followed here. She treated *Synnotia metelerkampiae* as a variety of *S. variegata*, but I prefer subspecies rank because the two taxa are for the most part easily separated, and they appear biologically as well as morphologically distinct. Subspecies *variegata* has larger, more brightly colored flowers and smaller capsules with fewer, large seeds and is self-incompatible, whereas subspecies *metelerkampiae* has smaller, less brightly colored flowers and larger capsules with numerous fairly small seeds and is autogamous. In this latter taxon, the style divides opposite the anthers, and the stigmatic surfaces of the rather short style branches are in contact with the pollen throughout anthesis. In subspecies *variegata* the style branches are generally longer and held above the anthers.

1a. Flowers with upper tepal 25–30 mm long; anthers 5–7 mm long; style at least as long as or exceeding the anthers, and style branches 4–7 mm long spreading above the anthers ..... 13a. subsp. *variegata*

1b. Flowers with upper tepal 14–17 mm long; anthers 3–4 mm long; style not exceeding the anthers, and style branches 2–3 mm long and tangled in the anthers ..... 13b. subsp. *metelerkampiae*

13a. Subspecies variegata

Sparaxis wattii Harvey, Gen. S. African Pl. ed. 1: 33. 1838. TYPE: South Africa. Cape: without precise locality, *Watt s.n.* (holotype, TCD; isotypes, GH, K). Figure 3A.

Plants 10–18(–30) cm high. *Spike* 3–8-flowered, the branches always with fewer flowers; *bracts* 20–25 mm long. *Flowers* either predominantly purple with the throat and bases of the lower tepals yellow or predominantly yellow with the upper tepals and the tips of the lower tepals becoming purple; *perianth tube* with the cylindric part 30–32 mm long, the upper part ca. 12 mm long, slightly inflated, ca. 12 mm wide at the mouth; *tepals* with the upper 25–30 mm long, 16–18 mm at the widest, upper laterals ca. 20 mm long, ca. 10 mm wide, the lower tepals united for 5–7 mm more than the upper, ca. 12 mm long. *Filaments* ca. 20 mm long; *anthers* 6–7 long, whitish with purple on the angles. Style dividing near the apex of the anthers, the branches 4–5 mm long, usually arching above the anthers. *Capsules* 9–10 mm long,

5–6 mm diam.; *seeds* ca. 2 mm diam., brown, 5–6 per locule.

The large flowers have partly to predominantly yellow flowers. The tepals are at least tipped with violet and sometimes are predominantly violet with relatively little yellow coloration (the types of both *S. variegata* and the synonym *S. wattii* correspond to the latter). Perianth color, the larger size of the tepals and anthers, and a style that divides near the anther apices distinguish subspecies *variegata* from subspecies *metelerkampiae*. The longer style with the branches arched above the anthers makes self-pollination unlikely, but the subspecies is genetically self-incompatible. The relatively small capsules contain 5–6 large seeds per locule. Subspecies *variegata* is centered in the lower Olifants River valley between Clanwilliam and Bulshoek, and occurs in sandstone rocks, sometimes in the courses of temporary streams.

13b. Subspecies metelerkampiae (L. Bolus) Goldblatt, comb. et stat nov. Basionym: *Synnotia metelerkampiae* L. Bolus, Ann. Bolus Herb. 3: 77. 1923. Pole Evans, Fl. Pl. S. Africa 3: t. 98. 1923. *Synnotia variegata* var. *metelerkampiae* (L. Bolus) G. Lewis, Ann. S. African Mus. 40: 148. 1956. TYPE: South Africa. Cape: Eendekuil, *Metelerkamp s.n.* (holotype, BOL 16039; isotypes, K, PRE). Figure 3B.

Sparaxis orchidiflora Lodd., Bot. Cab. 11: t. 1099. 1825, nom. nud.

Sparaxis luteoviolacea Ecklon, Topogr. Verz. 27. 1827. nom. nud. (*Ecklon & Zeyher 76.8*, C, E, G, GH, P).

Plants 15–30 cm high. *Spike* 2–5-flowered; *bracts* 15–18 mm long. *Flower* violet-purple with cream to yellow (rarely reddish) markings on the lower tepals; *perianth tube* with the cylindric lower part 35–40 mm long, the upper part ca. 10 mm long, 6–7 mm wide at the mouth; *tepals* unequal, the upper largest and erect with the margins incurved, 14–17 mm long, 8–10 mm wide, the upper laterals 12 mm long, ca. 5 mm wide, directed forward in the upper half, the lower tepals united for 3 mm more than the upper, ± horizontal, ca. 12 mm long, 4–5 wide, flexed downward distally. *Filaments* 10–12 mm long, purple, reaching to the top of the tube or slightly exserted; *anthers* 3–4 mm long, purple. *Style* dividing opposite the lower part of the anthers, purple, branches diverging, 2–3 mm long, extending between the anthers. *Capsule* cylindric-trilobed, 12–15 mm long, 5 mm wide; *seeds* 1.3–1.6 mm diam., 10–12 per locule, brown.

Subspecies *metelerkampiae* has largely purple flowers with the lower tepals each with a white longitudinal streak, at the center of which is a pale yellow mark (reddish in the type figure). The tepals are smaller than those of typical subspecies *variegata*, and the style branches are short and in contact with the anthers. Greenhouse studies have shown that this form is fully self-compatible and sets full capsules with 10–12 seeds per locule without deliberate self-pollination.

There is some variation in flower size and coloration in *Sparaxis variegata* and it is not always clear to which subspecies populations are best referred. Lewis (1956) assigned large-flowered plants, irrespective of perianth color, to subspecies *variegata* and smaller-flowered plants to subspecies *metelerkampiae*. Some of the variation in perianth size may be due to growing conditions, but as Lewis pointed out, the existence of these variants makes it impossible to maintain *S. metelerkampiae* as a separate species, despite the striking differences, both in morphology and reproductive biology, in the extremes. *Sparaxis variegata* needs more study in the field and laboratory.

Subspecies *metelerkampiae* is relatively widely distributed in the western Cape, extending from Eendekuil and Piekeniers Kloof north through the Olifants River valley and the adjacent valleys of the Cedarberg north to the Gifberg, and the Nieuwoudtville Escarpment. It grows in sandy and stony ground in well-drained situations.

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